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INTERANNUAL VARIABILITY IN DOLPHIN HABITATS IN THE EASTERN TROPICAL PACIFIC, 1986–1990

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ADMINISTRATIVE REPORT LJ-91-42

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INTERANNUAL VARIABILITY IN DOLPHIN HABITATS IN THE EASTERN TROPICAL PACIFIC, 1986-1990

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ABSTRACT

We used canonical correspondence analysis (CCA), an eigenvector ordination technique that includes direct gradient analysis, to investigate habitat use by spotted, spinner, striped and common dolphins in the eastern tropical Pacific during 1986 - 1990. Data were collected during annual research vessel cruises conducted in August - November of each year. Environmental variables included in the analyses were: surface temperature, salinity, sigma-t, and chlorophyll, thermocline depth and thickness. The dominant pattern in the species-environment relationship (1st canonical axis) separated common dolphins from spotted and spinner dolphins, based on their associations with cool upwelling habitat and warm tropical habitat, respectively. The second axis separated whitebelly spinners from eastern spinners. Both occurred in tropical water, but were separated primarily by thermocline topography. The species - environment correlations were 0.67 on the first axis, 0.42 on the second. Overall, the environmental data explained 15% of the variance in the species data. For individual school types this ranged from 36% for common dolphins to 6% for striped dolphins. Interannual variability in the species data was small, but judged significant by a Monte Carlo randomization test. Residual interannual variance was insignificant after removing variance associated with environmental variables.

INTRODUCTION

The eastern tropical Pacific (ETP) supports a cetacean fauna that is both diverse and abundant, including over 25 species (Au and Perryman 1985, Leatherwood et al. 1982). It is a vast area, larger than the entire North Atlantic. Its waters are truly pelagic, except near a few islands and over a narrow continental shelf. Prior to the 1960's almost nothing was known of the distribution and ecology of the region's cetaceans beyond the summaries of catch localities from 19th Century fisheries for large whales (Townsend 1935).

By the late 1960's, it became clear that large numbers of dolphins were being killed in the ETP in tuna purse seine operations (Perrin 1969). The US government initiated a program at that time to place scientific observers on purse seiners to monitor dolphin mortality (Smith 1983). Beginning in 1974, research vessels were dispatched to the region to supplement the observer data (Holt et al. 1987). The combination of these efforts has produced unprecedented amounts of information on pelagic cetaceans.

In this study we focused on the dolphin species affected by the tuna fishery: spotted dolphins (Stenella attenuata), two subspecies of spinner dolphins (S. longirostris), "whitebelly spinners" and "eastern spinners" (Perrin 1990), striped dolphins (S. coeruleoalba) and common dolphins (Delphinus

delphis). Community - level patterns, including all other cetacean species occurring in the region, are considered in a separate paper (Reilly and Fiedler, in preparation).

Dolphin distribution patterns have been described from sighting and collection localities (e.g., Au and Perryman 1985, Evans 1975, Perrin 1975, Perrin et al. 1983, 1985). Au and Perryman (1985) studied cetacean habitats of the eastern tropical Pacific from sightings and oceanographic data collected during the northern winter. They described two complementary patterns, both with apparent links to the region's oceanography. One pattern, shown by common and striped dolphins, coincided with "upwelling-modified" conditions, found along the equator, and at the tropical terminations of eastern boundary currents off Baja California and the coasts of Ecuador and northern Peru (described in more detail below in Study Area). The second pattern, shown by spotted and spinner dolphins, coincided with largely tropical waters off Mexico, where warm, low-salinity surface waters occur over a strong, relatively shallow thermocline.

Reilly (1990) examined ETP dolphin distributions in the northern summer, and quantitatively tested Au and Perryman's habitat hypotheses. He found an apparent offshore shift in spotted, spinner and striped (but not common) dolphins coincident with seasonal shoaling of a thermocline ridge along 10 N (Fig. 1). This seasonal shoaling is part of the dominant pattern of seasonal change in the ETP, associated with the north-south movement of the Intertropical Convergence Zone between the trade winds (Fiedler 1991). Statistical tests supported the habitat hypotheses of Au and Perryman (1985) for spotted, spinner and common dolphins, but not for striped dolphins. In the summer striped dolphins occupied habitat that was geographically complementary with the habitats of both common and of spotted/spinner dolphins (Fig. 1). Striped dolphin habitat was not distinguishable statistically from either the upwelling-modified or tropical habitats with the variables used, indicating that other factors or processes act to separate these dolphins from the others.

Interannual variation in the region's oceanography is dominated by the quasi-periodic El Niño-Southern Oscillation (ENSO; Enfield 1989). Interannual variation exceeds seasonal variation in much of the ETP (Fiedler 1991). ENSO variability affects all of the patterns and processes so far identified with cetacean habitats. From this we hypothesized that dolphin distributions might change interannually in response to changes in the distribution of their habitats. If so, this could have important implications for the monitoring of trends in the animals' abundance now in progress from both research vessel surveys (Gerrodette and Wade 1991) and tuna vessel observer data (Anganuzzi and Buckland 1989).

The primary objective of this study was to examine inter-annual variability in dolphin habitats, defined by multivariate techniques, for the years 1986 - 1990. We also suggest methods for the use of habitat information in the monitoring of trends in cetacean abundance. That is, given a quantitative definition of habitat and a record of interannual changes in habitat distribution, can we contribute to a reduction in variance and/or bias in the monitoring of trends in abundance?

STUDY AREA

The basic physical features of the upper ocean in the eastern tropical Pacific have been described by Wyrtki (1966, 1967), and Tsuchiya (1974). Fiedler (1991) updated this description and summarized seasonal and interannual variability. Major surface water masses and currents are depicted in Figure 2.

Warm, low-salinity *Tropical Surface Water* is found in the center of the ETP. Cooler, higher-salinity *Equatorial Surface Water* is found south of about 3N. *Peru Current* and *California Current Waters* are found along the coasts of Peru-Ecuador and Baja California, respectively. The Peru and California Currents feed into the westward South and North Equatorial Currents (SEC, NEC). The North Equatorial Countercurrent (NECC) flows eastward between the NEC and SEC into the center of the *Tropical Surface Water* mass. The NECC is strong in September-December and weak or absent in February-April.

A permanent, shallow thermocline underlies most of the region, shoaling towards the coast (Wyrtki 1966). Zonal thermocline ridges are found below surface divergences in the SEC along the equator and between the NEC and NECC along 10N (Fiedler 1991). Upwelling driven by equatorward longshore winds off Peru and Baja California and by trade winds along the equator brings cold, nutrient-rich water from below the shallow thermocline (nutricline) into the surface layer. This nutrient input maintains optimal (saturating) concentrations of new nitrogen at the surface and results in high levels of new production in equatorial and eastern boundary current systems (Chavez and Barber 1987). Biological productivity is also enhanced by upwelling at the Costa Rica Dome (a quasi-permanent cyclonic eddy at the eastern end of the thermocline ridge along 10N; Wyrtki 1964, King 1986), and by intermittent, topographically-induced offshore winds at several points along the coast of Central America (e.g., the Gulf of Tehuantepec, McCreary et al. 1989).

Secondary and higher level productivity and standing stocks are generally high in areas of high primary productivity (Blackburn et al. 1970).Within this and other large oceanic regions, the abundance of animals from plankton to large nekton is patchy on a variety of spatial and temporal scales (Haury et al. 1978), with major consequences for the ecology of pelagic predators (e.g., Carr 1987).

DATA & METHODS

Field Data Collection.

Both dolphin sightings and oceanographic data were collected by two ships operating in different parts of the ETP from July 28 through December 6 each year from 1986 to 1990 (e.g., Holt et al. 1987). Track lines are shown in Fig. 3. The surveys were conducted at 10 knots (18.5 km/hr) with three observers simultaneously on watch. One observer covered each side of the ship with a pair of 25x ship's binoculars to search an arc from the ship's bow to about 100° to the beam. The third observer covered the track line with hand-held binoculars and the naked eye. Sightings were approached when necessary to allow estimation of numbers within groups and species identification (Holt and Sexton 1990).

While the ships were underway, surface temperature and salinity were recorded continuously by thermosalinograph (ODEC Model TSG-102, Inter-Ocean Model 541 or Seabird SEACAT Model 21). Vertical structure was sampled in two ways. XBTs were deployed 4 to 6 times daily (every 55 to 110 km). Twice daily, just before dawn and just after dusk, the ships stopped to deploy conductivity - temperature - depth instruments (CTDs) to 1000 m. Sea water samples were collected with Niskin rosettes for chlorophyll and nutrient analysis. Surface chlorophyll was monitored continuously with a Turner Designs Fluorometer calibrated from discrete samples drawn at the surface at least six times per day (see Fiedler et al. 1990 for more detail).

Analytic Methods.

We estimated dolphin abundance, as the number of schools sighted per distance searched, for each day for seven pod type categories (Table 1). These are the most frequently sighted types of dolphin schools in the region. They are also the types captured by the purse seine fishery. Only days with at least two hours of sighting effort (approximately 37 km) during periods of fair or better sighting conditions (Beaufort 5 or less) were used in the analyses. The distance searched in one day varied between 37 and 222 km. We analyzed each day's sightings in relation to environmental

conditions measured during that day.

Reilly (1990) found that dolphin habitats in the ETP could be defined statistically by a combination of thermocline depth, surface temperature and salinity (combined into sigma-t). We used these variables plus the following: an estimate of surface chlorophyll (log-transformed), a measure of thermocline thickness (the difference in depth between the 20° and 15° isotherms), and surface water density (sigma-t: Pickard and Emery 1982). Surface temperature, salinity and chlorophyll were averaged from the day's continuous sampling during sighting effort. Thermocline depth (represented by the depth of the 20°C isotherm: Donguy and Meyers 1987) and thickness were estimated from XBT casts made during or within a few hours of sighting effort. We included sigma-t, in addition to both temperature and salinity, in the multivariate analyses as a form of "product variable", to see if it contributed additional information for determining dolphin habitats. In summary, the six oceanographic variables considered were, 1) surface temperature, TEMP; 2) surface salinity, SAL; 3) surface density, SIGMAT; 4) thermocline depth, Z20; 5) thermocline strength, ZD; and 6) chlorophyll, LOGC.

We examined the effects of interannual variability by including years (scaled 1-5) as categorical variables. (More details on this are given below). Additionally, we examined the contribution of fixed geographic effects by including latitude and longitude in some analyses. All environmental variables (oceanographic and geographic) were normalized prior to multivariate analyses to remove effects from differing scales of measurement.

The relationships between dolphin school distributions and environmental variation were analyzed using canonical correspondence analysis (CCA; Ter Braak 1986). We used the computer program CANOCO (Ter Braak 1985). Correspondence analysis is an eigenvector ordination technique, similar to principal components analysis, that can be used to investigate community structure. These methods extract dominant, orthogonal axes of variation in abundance indices for multiple species at multiple sites. Typically, the ordination axes are then interpreted indirectly with the help of external knowledge and data on environmental gradients, either qualitatively or with regression methods (Gauch 1982).

In contrast to principal components analysis and other linear methods, correspondence analysis (CA, also called reciprocal averaging) fits non-linear Gaussian (unimodal) models to the species abundance data. Canonical correspondence analysis is an extension of CA in which the species ordination is done directly and iteratively in relation to environmental variables. CCA is an efficient

ordination technique when species have bell-shaped response curves or surfaces with respect to environmental gradients (Ter Braak 1986), which is consistent with general ecological knowledge (e.g., Whittaker et al. 1973). The models and algorithm used in CCA are summarized in the Appendix.

As part of the species-environment ordination, CCA estimates a series of site scores (here, site = day) that are linear combinations of the environmental variables that maximize the species-environment correlation. One set of site scores is estimated for each canonical ordination axis. The interpretation of environmental patterns represented by the axes is made from the correlation coefficients and the multiple regression or "canonical" coefficients of the original environmental variables with the canonical axes (Ter Braak 1986).

The results of canonical correspondence can be best interpreted from an ordination "biplot", on which species and sites can be represented by points and environmental variables by arrows. The biplot displays the site-weighted mean species scores or "optima" on two canonical axes, usually the first two, which explain the majority of the variance. The directions and relative lengths of the arrows for environmental variables represent their contributions to the ordination. More important environmental variables are therefore represented by longer arrows.

Community ordination was not our primary objective, but we used CCA for three reasons. It provides a quantitative definition of habitat for each species/stock in reduced dimensionality. The method estimates habitats using a non-linear, unimodal model, avoiding the unrealistic assumption of a linear relationship between animal abundance and environmental gradients. CANOCO is also insensitive to a high frequency of zero observations (Ter Braak 1985), typically found in animal survey data.

In assessing the contributions of environmental variables we took the liberal approach of retaining variables unless they were almost entirely redundant with other, more influential variables. That is, a variable of marginal significance was not excluded if the apparent direction of its influence was different from the other environmental variables. Model over-specification was not a problem, because we had 956 cases and a maximum of only 13 environmental variables (considering years as five dummy variables). We did not use stepwise procedures, which appear to offer an objective approach to variable selection, but are notoriously problematic for other reasons (e.g. Pimentel 1979, pp. 42-43).

We examined the importance of interannual variability in two related ways. First, as noted above,

we included years as categorical explanatory variables, in addition to the oceanographic variables. The importance was then gauged by comparing ordination results to those with just the oceanographic variables. Second, we removed the variance associated with the environmental variables (by defining them as covariables), and then extracted axes associated with variance among years, to test for interannual differences in the species data not associated directly with interannual environmental variation.

The significance of an ordination axis was determined by testing the null hypothesis that its eigenvalue was not different from zero. The procedure used was a Monte Carlo randomization test (e.g., Hope 1968) supplied with the program CANOCO. This procedure randomly associated sets of environmental variables from one case with sets of species data from another, then extracted canonical axes, and estimated their eigenvalues. The procedure was run 1,000 times to produce a reference set of eigenvalues representing random variability. The significance of the eigenvalues from the original data was determined by comparison to these distributions.

We extended the use of canonical correspondence analysis in two ways for our study of interannual variation in cetacean habitats. First, we mapped the spatial distributions of the site scores from the first two CCA axes, lightly smoothed and contoured. We then plotted the localities of cetacean sightings over these contours to allow visual appraisal of species-environment patterns. We did this as an alternative to plotting species and hundreds of sites together on a biplot, which we found to be uninformative. Second, we suggest two ways in which the results of the canonical correspondence analysis can be used in the monitoring of trends in cetacean abundance.

RESULTS

The research vessels searched a total of 140,597 km (Fig. 3), and recorded a total of 2014 sightings of dolphin schools of the 7 types considered here, during five annual cruises, 1986 through 1990 (Table 1). The environmental data used include continuous temperature, salinity and fluorescence measurements along most of the trackline, 17,303 surface chlorophyll measurements, 4,726 XBT deployments and 1,596 CTD stations (Table 2).

Table 3 gives the weighted correlation matrix for the six oceanographic variables, the four species axes and four environmental axes from the CCA. The "species-environment" correlations are the values for equivalent axes, e.g., the correlation between the dominant species axis (no. 1) and the

first environmental axis is 0.67. The correlation between the second axes is 0.45, and so on.

The eigenvalues for the ordination axes indicate that only the first two are important (Table 4). Axes 3 and 4 together represent only 6% of the variation of the species - environment data. Ter Braak (1985) suggests that eigenvalues less than 0.02 be disregarded. The first axis accounts for 70% of the variance extracted, the second accounts for 24%, together they represent 94%. Further results and discussion therefore relate to only axes 1 and 2.

The relationships between most of the species categories of interest and the first two environmental axes were unimodal (Fig. 4), satisfying a primary assumption of CCA. One exception was common dolphins on axis 1, where there is evidence of bimodality.

The Monte Carlo randomization test resulted in rejection of the null hypothesis of no relationship between the species encounter rates and the environmental data (H_o λ=0). One thousand random permutations produced no ordinations with a trace (eigenvalue total) larger than the observed 0.443, giving a P-value < 0.001. The same was true for the first axis alone; no random permutation had an eigenvalue larger than the observed 0.309, again giving a P-value < 0.001. These results indicate that the probability of a Type I error is less than 0.1%. (The CCA program, CANOCO, provided this test only for the trace and first axis, so no test was done for subsequent axes).

This ordination explained 14.7% of the variance in the dolphin school abundance data as a whole, with a range from 33.5% for common dolphins to just 5.1% for whitebelly spinner dolphins (Table 4).

The species-environment biplot (Fig. 5a) displays the ordination results. Figure 5b shows the ordination with species tolerances, but without the visual distraction of the environmental vectors. The first axis separates common dolphins from all school types containing spotted and spinner dolphins. Positive scores on axis 1 are associated with cooler temperature (r= -0.88, Table 3), a thermocline that is shallower (i.e. smaller Z20, r= -0.70), yet weaker (larger difference in depth between 20° and 15°C isotherms, r = +0.45), denser surface water (higher sigma-t, r = +0.61) and high chlorophyll (r= +0.49). We interpret these as characteristics of a "cool upwelling" habitat, as found in Equatorial and Peru/California Current Surface Waters. This is the preferred habitat of common dolphins. Negative scores on axis 1 are associated with warm temperature, a deeper and stronger thermocline, and lower chlorophyll, as found in less productive Tropical Surface Water.

Site or species scores on axis 2 are uncorrelated with scores on axis 1, by definition. Positive axis 2 scores are associated with a relatively shallow thermocline (r= -0.63, Table 3) and high chlorophyll (r= +0.40) as for axis 1, but also with warmer temperatures and lower salinity (lower sigma-t) rather than cool temperature. We interpret these as characteristics of a "coastal tropical" habitat found along the coast of Central America, where the surface layer is more stratified and upwelling is more intermittent and localized than in the "cool upwelling" habitat.

Whitebelly spinners, alone and with spotted dolphins, had large negative axis 2 scores, while eastern spinners with spotted dolphins had positive scores. There was a strong separation on axis 2 between mixed schools of spotted dolphins with whitebelly and eastern spinners. Spotted dolphins alone had near-zero axis 2 scores. Striped dolphins loaded near the origin of both axes, indicating either that this is near their "optimum" habitat or that their distribution is unrelated to the environmental patterns represented in the canonical axes. The low "R^2" for striped dolphins (Table 4), and their spatial distribution (below) support the latter interpretation.

The spatial distributions of yearly axis 1 scores are mapped in Figure 6. "Cool upwelling" habitat (positive scores) is shaded to allow quick appraisal of changes between years. In 1986, "cool upwelling" habitat was found along the equator to 130W, north of the equator to about 10N along the coast of Central America, and off the coast of Baja California. In 1987, "cool upwelling" habitat south of Baja California did not extend west of 110W or north of 4N, except in the Gulf of Panama. The study area was dominated by warm, low-productivity tropical water (negative axis 1 scores). This change was caused by a moderate El Niño event that began in late 1986 and lasted through 1987 (Kousky and Leetmaa 1989). In 1988, "cool upwelling" water extended far north of the equator and south of Baja California, considerably reducing the area covered by tropical water. 1988 was a strong anti-El Niño or La Niña year (Leetmaa 1990, Fiedler et al. 1992). In 1989 and 1990, conditions represented by axis 1 scores returned to a state similar to 1986.

Also plotted in Fig. 6 are sighting localities for spotted and common dolphins. Spotted dolphins occurred mostly in negative areas, common dolphins in positive areas, but with some overlap. In 1987, with "cool upwelling" conditions contracted eastward and southward at the equator, common dolphins occurred in the southern ETP only in the far east off South America. In 1988 when these conditions were strongly established along the equator to the western extent of the study area, common dolphins occurred in equatorial waters as far west as 110W.

Spatial distributions of yearly axis 2 scores are mapped in Figure 7, with "coastal tropical" habitat (positive scores) shaded. "Coastal tropical" habitat overlaps "cool upwelling" habitat in eastern equatorial water and also is found in small patches along the edges of the study area near the subtropical oceanic gyres north and south of the equator. Interannual variation along this axis is not strongly related to ENSO variability. The area with positive axis 2 scores ("coastal tropical" habitat) was small in 1986 and 1987, increased in 1988 and again in 1989, and showed some diminishment in 1990. Whitebelly spinners were seen almost exclusively in waters with negative axis 2 scores (Figures 5 & 7). Eastern spinners ranged throughout both positive and negative areas, with a modest majority occurring in positive areas. They were less closely associated with this axis than whitebelly spinners (Fig. 5) and seemed to be found in the eastern (more coastal) part of the warm tropical habitat defined by negative axis 1 scores.

Interannual Variability

Inclusion of categorical variables representing the five sampled years, in addition to the six oceanographic variables, resulted in a very slight increase in the percent of variance explained for the dolphin data (14.7% to 15.1%, Table 5). An ordination biplot from this analysis (Figure 8) shows that the centroid for 1988 (year 3) loads farthest from the origin. Its location represents the cooler, more productive conditions associated with the 1988 La Niña.

An analysis including just years as categories, without oceanographic variables, explained only about 2% of the dolphin variance, but the dominant eigenvalue and trace were both significantly different from zero (Monte Carlo P-values = .01 and .02, respectively). After extraction of the variance associated with the six oceanographic variables (by defining them as covariables) the ordination was not significant (Monte Carlo P = .058, Table 5).

Fixed Geographic Effects

Inclusion of latitude and longitude in addition to the six oceanographic variables produced a notable increase in dolphin variance explained, from 14.7% to 20.5% (Table 5). The amount of additional influence indicated for fixed geographic effects varied substantially among school types. The largest increases were for whitebelly spinners, alone and with spotted dolphins. No improvement in explaining variance was made for schools of spotted dolphins alone.

DISCUSSION

The ordination results were generally consistent with past studies of ETP cetacean ecology. The placement of common dolphins into "cool upwelling" habitat is consistent with results reported by Au & Perryman (1985), and Reilly (1990). The placement of spotted and spinner dolphins in contrasting habitat (essentially warm tropical water) is also as reported earlier. Consistency with results of Reilly (1990) is not surprising, because that study shared data from 1986 and 1987 with this study, but is somewhat reassuring because different analytical techniques were used.

The second axis successfully separated eastern spinners from whitebelly spinners. This separation was even clearer between eastern spinners co-schooled with spotted dolphins and whitebelly spinners co-schooled with spotted dolphins. The placement of whitebelly spinners in habitat with a deeper thermocline follows from their more offshore distribution and the general tendency for the thermocline to shoal to the east in the ETP. Spotted dolphins alone were placed intermediate to these mixed schools. If this is a general pattern it suggests that the two mixed school types of spotted and spinner dolphins are utilizing habitats as different as those used by separate species (e.g. common dolphins and spotted dolphins on axis 1). These results are also consistent with the hypothesis that the morphological distinctness of the endemic eastern spinner subspecies reflects adaptation to local habitat conditions (Dizon et al. 1991).

The environmental patterns represented in the CCA axes are very similar to simple ordinations made by principal components analysis (PCA). For example, site scores of the first component of a PCA of TEMP, SAL, Z20 and LOGC for 1986 (Fig. 9) display spatial patterns quite close to those from the first CCA axis for that year (Fig. 6a). This shows that ETP cetaceans are responding to the major components of environmental variation, and allows straightforward interpretation of environmental processes represented by the CCA axes. The linear combinations of environmental variables extracted by CCA are in fact weighted principal components, the weights being functions of the species data (Ter Braak 1987). This result suggests that ETP cetaceans are exhibiting habitat separation along the longest axes of environmental variability.

The maps in Figures 6 and 7 are imprecise representations of species-environment patterns derived by CCA for two reasons. First, the maps show only presence-absence, while we used an effort-corrected index of abundance (daily encounter rate) in the CCA. Second, the contouring requires some smoothing and interpolation between sites, while the CCA compared abundance indices only to environmental variables measured during the same day, along the same track lines where the

cetaceans were sighted. These species are apparently separating more strongly on a smaller scale than we could effectively represent on the maps. A further consideration is that the scaling of axes for biplot presentation was done using a method in which the canonical scores (as plotted on the maps here) are re-scaled to produce biplot locations (Ter Braak 1988). The resulting ordination gives an accurate relative placement of species centroids, but does not allow direct projection of centroids or tolerances onto canonical axis values as mapped in Figures 6 and 7.

Another result of the CCA was that the small but significant interannual variation in the species data was effectively accounted for by interannual variation in the environment. This was demonstrated by the low eigenvalue ($\lambda = 0.02$, $P = 0.06$) for interannual differences after extracting variance associated with the six oceanographic variables. This result does not necessarily apply to total population abundances, however, since we did not include school size estimates in our species data.

The species-environment correlations observed were quite high: .67 for the first species & environment axes, .42 for the second axes. However, variation extracted by the canonical correspondence analysis accounted for just 15% of the total encounter rate variance. (This was increased to over 20% when fixed geographic effects were considered). This modest explanatory power is in fact fairly good, given the unknown but surely large sampling variability inherent in daily encounter rates. Dolphin schools are very mobile and patchily distributed; these animals are known to have complex social and behavioral interactions with their own and other species, and are not planktonic entities, passively floating along with a set of oceanographic conditions.

Explanatory power for common dolphins was surprisingly high; 36% with the six oceanographic variables, and 42% with fixed geography included. This result indicates that common dolphins have the tightest association with the environmental variables of the seven school types studied here. It also demonstrates the robustness of CCA, considering the bimodal distribution of common dolphins on axis 1 (Fig. 4).

The notable increase in performance for whitebelly spinner dolphins resulting from consideration of fixed geography raises interesting questions. Are they directly responding to some geophysical cue, such as magnetic anomalies? (Kirschvink et al. 1986, Klinowska 1985). Or, does this result simply reflect orientation to oceanographic features or processes not represented in our data?

We suggest two approaches to use the results of this study in trend monitoring for ETP cetaceans. Other, perhaps more sophisticated approaches are possible. We present these only as examples. The

most straightforward approach, involving minimal assumptions, would be to post-stratify the data for each year separately, based on the spatial distribution of CCA axis scores and the weighted mean and sd of those scores for the species of interest. Species/stocks that have similar means and sd's could use common strata. For example, separate strata could be defined using axis 1 for common and spotted dolphins. Axis 2 could be used to provide strata for whitebelly spinner dolphins. Because we have probability distributions for the occurrence of these species along the canonical axes, we would not be limited to use just two strata but could use three or four. After the data were stratified based on the species annual habitat distributions, standard line transect methodology would be followed. This is generically similar to the post-stratification approach taken by Anganuzzi & Buckland (1989) to reduce bias in estimates of dolphin abundance from tuna vessel observer data.

A second possible approach would quantify the amount of habitat available within the study area each year, for each species/stock. The simplest quantification scheme would define only two strata for each. The cut-point between strata could be the 95% limit of the species/stock's distribution on the axis, or, less conservatively, the appropriate upper or lower quartile. More complex schemes using more than two strata could be developed, as with the post-stratification, based on additional information in the species probability distributions. The amount of any stratum available in a year could be quantified by, say, lightly smoothing and interpolating the CCA site scores (to provide values for all locations) and "sampling" the distribution with the actual cruise tracks for the year. If for example common dolphin habitat was to be defined as axis 1 > [some value], the amount of ocean sampled with axis 1 > [some value] in 1986 could be scaled as 1.0. The amount sampled in subsequent years could be scaled to the 1986 amount. The result would be a vector of values representing the amount of common dolphin habitat available within the ETP by year. This vector could then be applied to the encounter rate portion of the line transect abundance estimate for each year to account for changing availability of common dolphin habitat. If interannual differences were subsequently observed in the line transect abundance estimates, we could be more confident that they represent real changes in abundance, rather than just apparent changes due to spatial redistribution relative to sampling effort following habitat shifts.

Fiedler and Reilly (1991) applied the CCA ordination approach developed here to investigate interannual variability in abundance indices for ETP dolphins estimated from tuna vessel observer data. They calculated annual indices of habitat quality for each dolphin species targeted by the tuna fishery, for the years 1975 - 1989, compared these habitat indices to Anganuzzi et al.s (1989, 1991) abundance estimates. They used a sub-set of three environmental variables from those used here, to enable use of existing, large data bases on oceanography of the ETP, to allow computation of

environmantal axes for years prior to 1986, They found that environmental variability does appear to influence the abundance estimates of some species.

We are now working on using environmental data to reduce error in dolphin abundance estimates derived from research vessel or tuna vessel sightings data. Gerrodette et al. (1991) applied the results of this study in a preliminary attempt to account for movements in and out of the study area when estimating total abundance of dolphins.

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APPENDIX. Summary of models and alogrithm used in canonical correspondence analysis, from Ter Braak (1986).

Notation

Y_{ik}	is the abundance of speices/stock k at site i
Y_{+k}	is the total abundance for species k (k=1,m)
Y_{i+}	is the total abundance of all species at site i (i=1,n)
x_i^*	is the site score for i from the species data
x_i	is the score for site i from the environmental data
$\mathbf{x}$	is a column vector of the x_i
$\mathbf{x}^*$	is a column vector of the x_i^*
λ	is the eigenvalue of the ordination axis
μ_k	is the weighted mean for species k
$\mathbf{b}$	is a column vector of regression coefficients
$\mathbf{R}$	is a diagonal n × n matrix with Y_{i+} as the (i,i)-th element
$\mathbf{Z}$	is an n x (q+1) matrix containing the environmental data and a column of ones

Transition Formulae of CCA

$$\lambda\mu_k = \sum_i Y_{ik}x_i/Y_{+k} \qquad (1)$$

$$x_i^* = \sum_k Y_{ik}\mu_k/Y_{i+} \qquad (2)$$

$$\mathbf{b} = (\mathbf{Z'RZ})^{-1}\mathbf{Z'Rx^*} \qquad (3)$$

$$\mathbf{x} = \mathbf{Zb} \qquad (4)$$

Algorithm of CCA

Step 1. Start with arbitrary but unequal site scores (x_i);

Step 2. Calculate species scores (μ) by weighted averaging of site scores (Eq. 1);

Step 3. Calculate new site scores (x_i^*) by weighted averaging of species scores (Eq. 2);

Step 4. Obtain regression (canonical) coefficients by weighted multiple regression of the scores on the environmental variables (Eq. 3). The weights are the site totals (Y_{i+}).

Step 5. Calculate new site scores (Eq. 4); center and standardize them ($\sum_i Y_{i+}x_i = 0$ and $\sum_i Y_{i+}x_i^2 = 1$);

Step 6. Stop when new site scores sufficiently close to previous iteration, otherwise go to Step 2.

Table 1. Search effort and number of cetacean schools recorded by year, 1986 - 1990, from the Monitoring of Porpoise Stocks expedition in the eastern tropical Pacific.

	YEAR					
	1986	1987	1988	1989	1990	Total
Km. Searched	28,917	27,735	24,224	27,323	32,398	140,597
Number Sightings of						
Spotted dolphins	71	85	47	78	78	359
Common dolphins	57	41	73	59	54	284
Spotted with Eastern Spinner	44	40	33	51	33	201
Spotted with Whitebelly Spinner	33	29	23	24	15	124
Eastern Spinner	27	18	6	19	13	83
Whitebelly Spinner	8	10	18	8	10	54
Striped dolphins	158	180	206	213	152	909
Rough-toothed dolphins	32	26	40	37	26	161
Bottlenose dolphins	95	80	64	67	78	384
Pilot whales	44	49	56	59	65	273
Pilot whales with Bottlenose dolphins	16	18	23	21	22	100
Risso's dolphins	37	61	44	46	33	221
Sperm whales	51	49	33	45	30	208
Blue whales	5	5	6	11	9	36
Byrde's whales	20	30	28	23	36	137
Other Baleen whales	37	39	46	56	94	272
Killer whales	12	12	11	15	15	65
Unid. Beaked whales	36	23	31	16	19	125
Unid. Mesoplodon	10	29	16	23	31	109
Cuvier's Beaked whales	22	17	16	32	25	112
Fraser's dolphins	5	8	6	6	7	32
Pygmy Killer whales	1	10	7	7	11	36
False Killer whales	10	13	4	7	7	41
Melon-headed whales	5	4	3	3	3	18
Coastal Spotted dolphins	12	8	2	2	2	26
Pygmy Sperm whales	50	17	21	32	9	129
White-sided dolphins	1	2	5	4	1	13
Totals	899	903	868	964	878	4512

Table 2. Oceanographic data from the Monitoring of Porpoise Stocks expedition, 1986-1990, used in the canonical correspondence analyses.

	1986	1987	1988	1989	1990	Total
km Surface Temperature, Salinity	28,917	27,735	24,224	27,323	32,398	140,597
Surface Chlorophyll Measurements	3,763	1,927	3,613	3,552	4,448	17,303
XBT Measurements (Drops)	1,144	1,160	835	778	809	4,726
CTD Measurements (Stations)	244	280	352	352	368	1,596

Table 3. Correlation coefficients among environmental variables, canonical species axes and environmental axes estimated by a canonical correspondence analysis of cetaceans in the eastern tropical Pacific during 1986 - 1990. Values marked with an * are significantly different from zero at $\alpha \leq 0.05$.

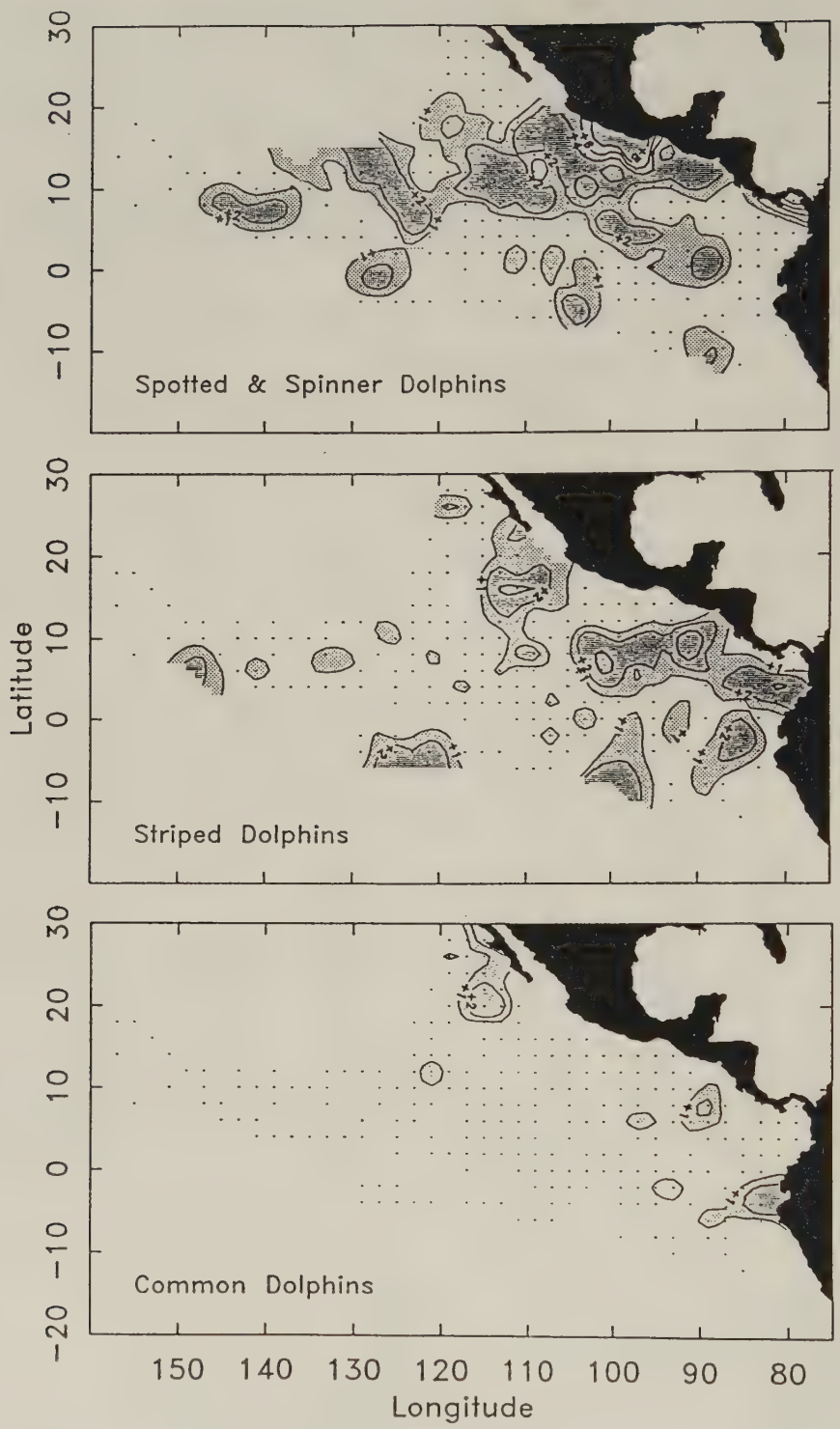
	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4	ENVI AX1	ENVI AX2	ENVI AX3	ENVI AX4	TEMP	SAL	LOGC	SIGMAT	Z20
SPEC AX1	1.0000												
SPEC AX2	.0080	1.0000											
SPEC AX3	.0070	-.0318	1.0000										
SPEC AX4	.0267	.0202	-.0428	1.0000									
ENVI AX1	.6681*	.0000	.0000	.0000	1.0000								
ENVI AX2	.0000	.4137*	.0000	.0000	.0000	1.0000							
ENVI AX3	.0000	.0000	.1844	.0000	.0000	.0000	1.0000						
ENVI AX4	.0000	.0000	.0000	.0944	.0000	.0000	.0000	1.0000					
TEMP	-.5895*	.1406	-.0120	.0243	-.8825*	.3399*	-.0649	.2573*	1.0000				
SAL	.0608	-.1099	.0384	-.0575	.0911	-.2657*	.2084	-.6089*	-.4747*	1.0000			
LOGC	.3236*	.1370	-.0934	-.0527	.4843*	.3311*	-.5066*	-.5579*	-.3697*	-.0209	1.0000		
SIGMAT	.4066*	-.1618	.0155	-.0433	.6086*	-.3911*	.0838	-.4589*	-.8892*	.8186*	.2280	1.0000	
Z20	-.4685*	-.2666*	.0336	-.0126	-.7013*	-.6443*	.1826	-.1336	.3921*	.0811	-.5103*	-.2023	1.000

Table 4. Ordination results from a canonical correspondence analysis of dolphin abundance and oceanographic conditions (surface temperature, salinity, sigma-t, chlorophyll, thermocline depth and thermocline strength) in the eastern tropical Pacific, August - November, 1986 - 1990. "S-E Total" is the sum of the species-environment eigenvalues, i.e. the species variation related to the environmental variables. "Overall Total" is the total of all variation in the species encounter rate data. P-values are from a Monte Carlo randomization test with 1,000 repetitions.

	CANONICAL AXES					
	1	2	3	4	S-E Total	Overall Total
Eigenvalues	0.309	0.107	0.020	0.005	0.443	3.002
P-values	<.001				<.001	
Species-environment correlations	0.669	0.415	0.196	0.120		
Cumulative percentage variance						
of species-environment relation	69.8	93.9	98.4	99.5		
of total species data	10.3	13.8	14.5	14.7		
of Spotted dolphin	7.9	7.9	8.1	8.1		
of Common "	33.7	34.9	35.5	35.5		
of Spotted & Eastern Spinner "	13.1	22.2	22.3	22.5		
of Spotted & Whitebelly Spinner "	8.3	9.3	9.5	9.7		
of Eastern Spinner "	6.6	7.4	7.4	8.3		
of Whitebelly Spinner "	0.9	3.7	4.8	5.1		
of Striped "	1.7	2.8	5.9	5.9		

Table 5. Comparative ordinations from canonical correspondence analyses of seven types of dolphin school in the eastern tropical Pacific, with six different sets of environmental variables. Set 1 = surface temperature (SST), thermocline depth (Z20) and thermocline strength (ZD). Set 2 = SST, Z20, ZD, surface salinity (SAL), surface chlorophyll (LOGC) and surface density (SIGMA-T). Set 3 = Set 2 plus years (1-5) as categorical variables. Set 4 = Set 2 plus latitude and longitude. Set 5 = Set 2 plus both latitude & longitude and years. Set 6 = years (1-5) as categorical variables, after removing variance associated with all other environmental variables (Set 5).

	ENVIRONMENTAL VARIABLE SET					
	1	2	3	4	5	6
Eigenvalue sum	0.384	0.443	0.464	0.622	0.644	0.022
P-value	<.001	<.001	<.001	<.001	<.001	0.058
Percent variance accounted for:						
of total species data	12.8	14.7	15.1	20.5	21.1	0.9
of spotted dolphin	7.8	8.2	8.8	8.8	9.6	0.8
of common dolphin	32.6	35.5	36.2	41.2	42.2	1.0
of spottted/e. spinner	18.8	22.5	22.8	25.0	25.3	0.3
of spoted/wb. spinner	9.2	9.6	9.9	16.4	17.3	1.0
of e. spinner	7.5	8.3	9.5	10.4	11.2	0.9
of wb. spinner	3.6	5.0	6.4	20.0	20.3	0.3
of striped dolphin	1.9	5.9	6.6	12.6	13.8	1.9



Fgure 1. Dolphin distributions in the northern summer in the eastern tropical Pacific, from Reilly (1990). Contours are for encounter rates per 185 km searched. Dots represent centers of 2° squares in which there was at least 185 km search effort.

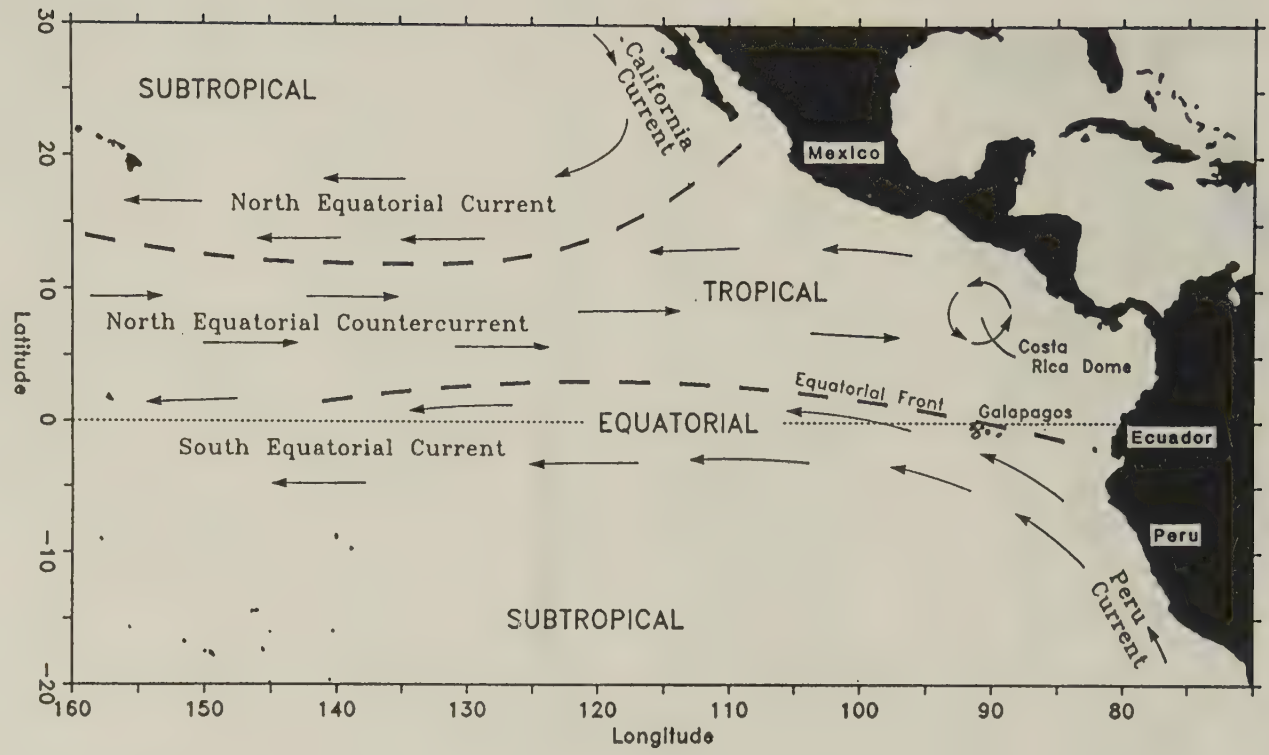


Figure 2. Schematic representation of the surface circulation and water masses of the eastern tropical Pacific.

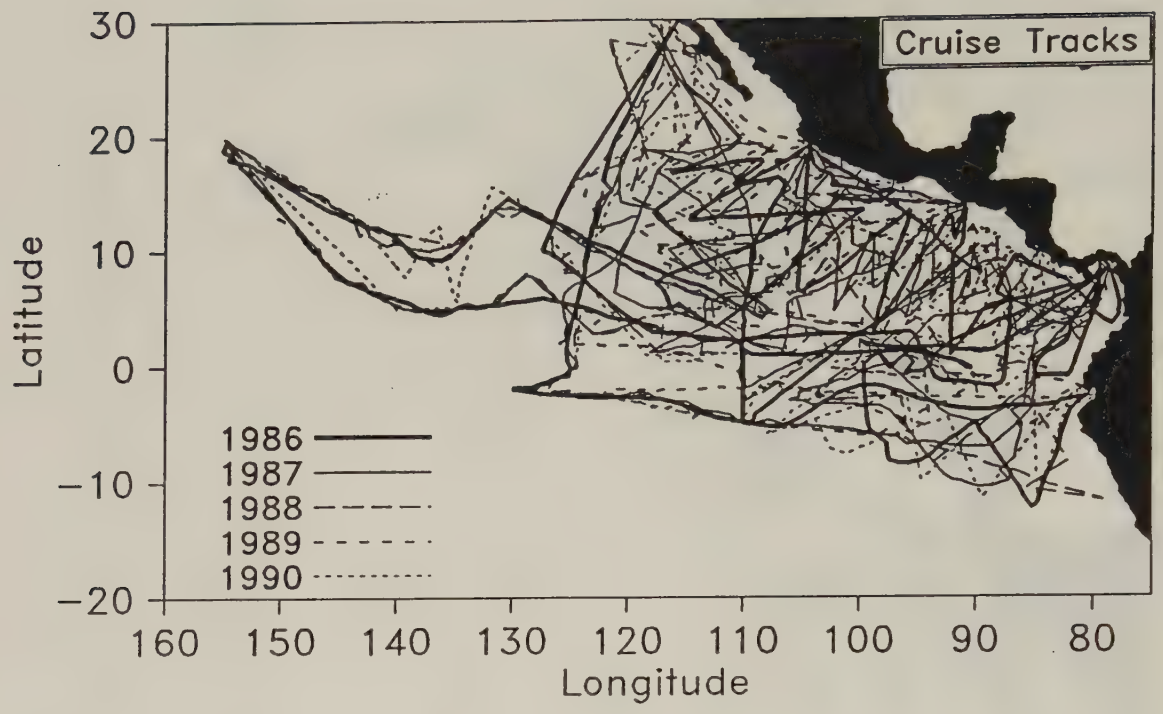
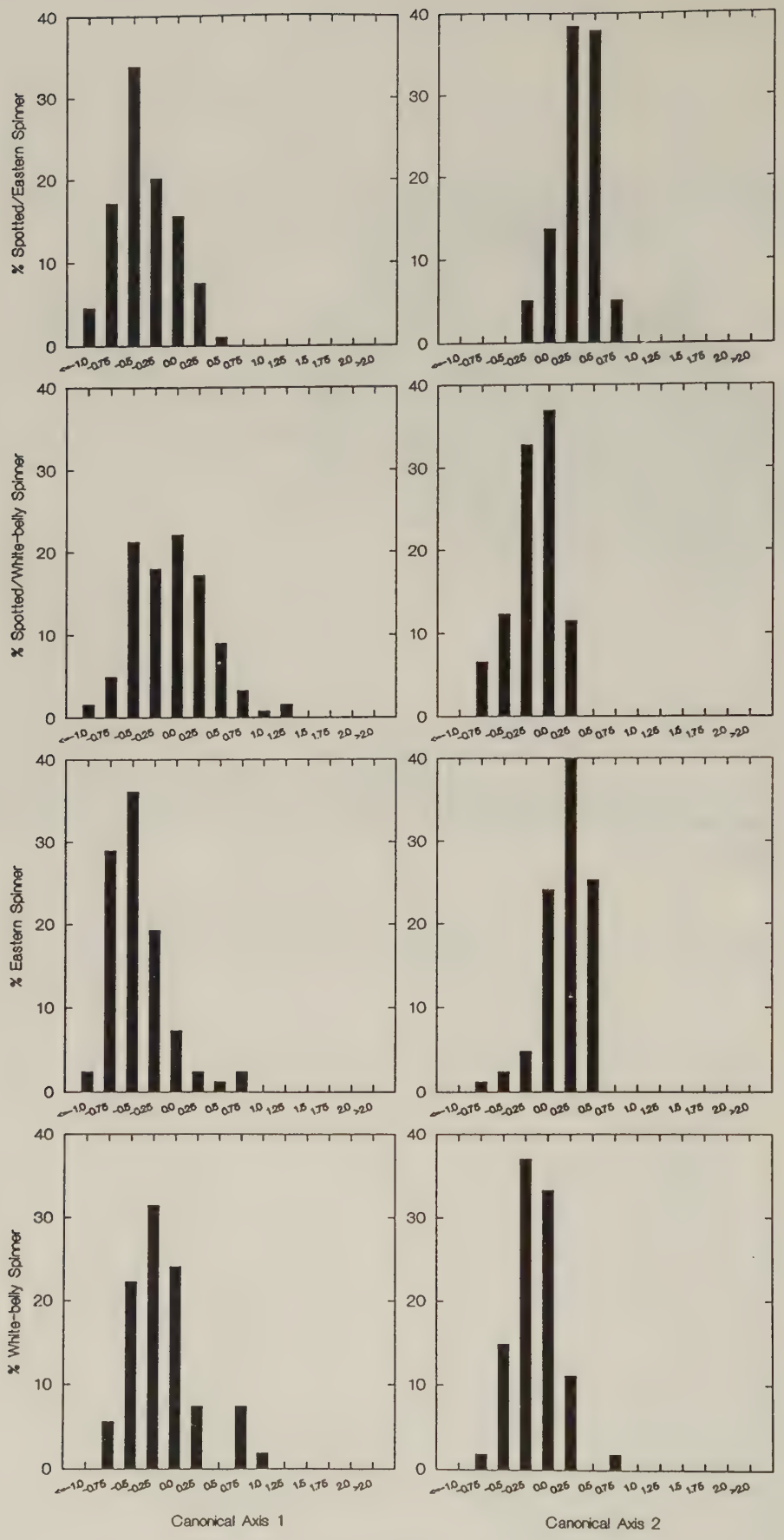


Figure 3. Cruise tracks of R/V David Starr Jordan and McArthur during August - November, 1986 - 1990.

Figure 4. (Following page) - Frequency histograms, transformed to percentages, of the first two environmental axis scores in areas where cetaceans were sighted for 7 species/stocks.


% Spotted/Eastern Spinner
% Spotted/White-belly Spinner
% Eastern Spinner
% White-belly Spinner
0
10
20
30
40
<-1.0 -.075 -.05 -.025 0.0 .025 .05 .075 1.0 1.25 1.5 1.75 2.0 >2.0
Canonical Axis 1
Canonical Axis 2

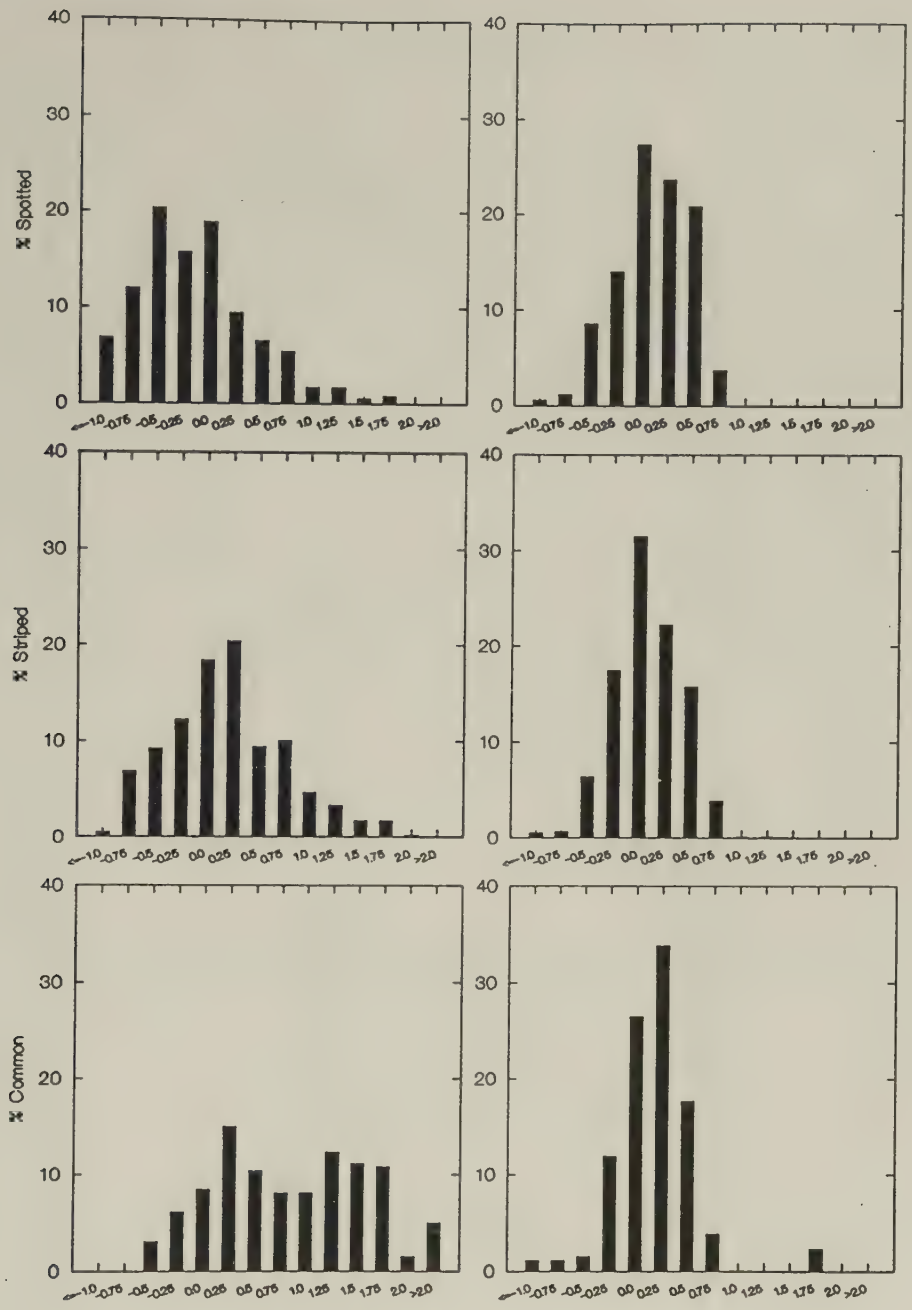


Figure 4. (Continued) - Frequency histograms, transformed to percentages, of the first two environmental axis scores in areas where cetaceans were sighted for 7 species/stocks.

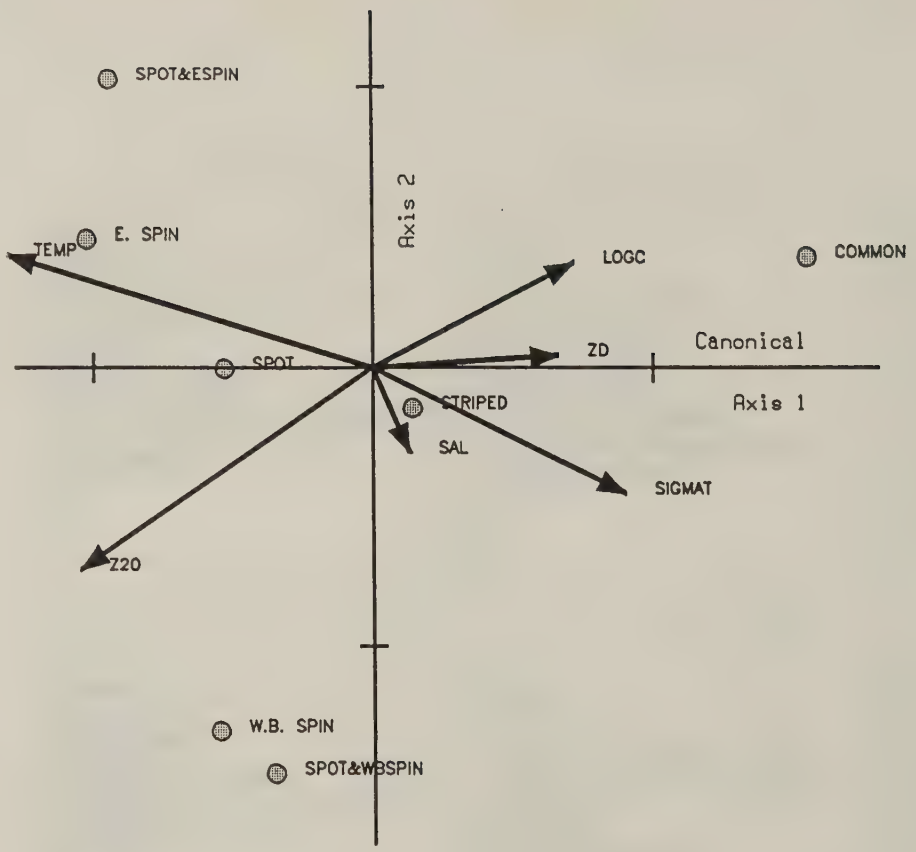


Figure 5a. Ordination results from canonical correspondence analysis of cetacean species/stocks and environmental conditions in the eastern tropical Pacific. (a) Biplot of first two species canonical axes and environmental variables. The environmental variables, represented by arrows, are: surface temperature (TEMP), surface salinity (SAL), thermocline depth indexed by 20°C isotherm depth (Z20), thermocline strength, indexed by the difference in depth between the 20C and 15C isotherms (ZD), surface water density (SIGMAT), and surface chlorophyll, log-transformed (LOGC). These two axes represent 94% of the species-environment variance, 15% of the total encounter rate variance.

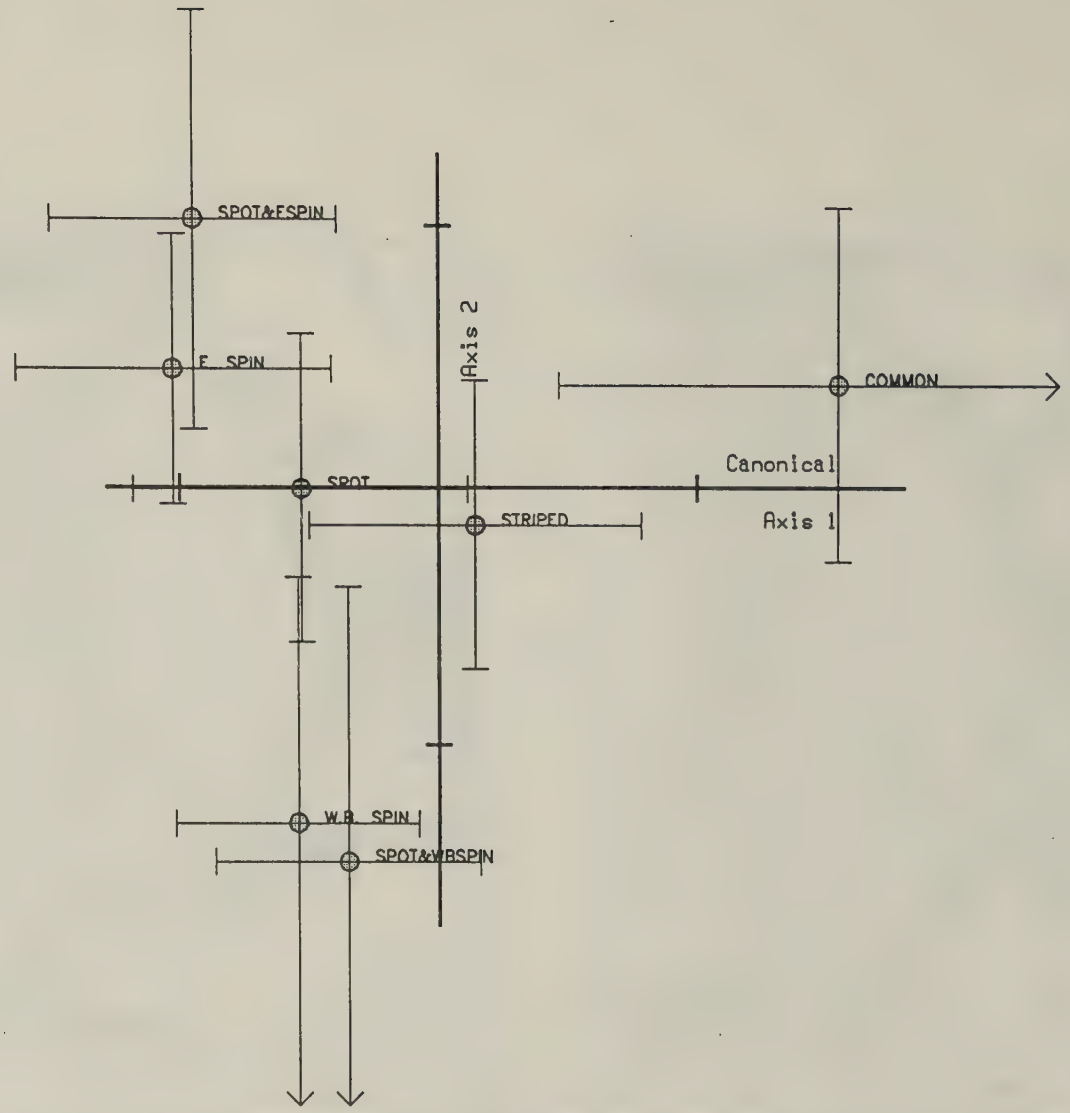


Figure 5b. Ordination results from canonical correspondence analysis of cetacean species/stocks and environmental conditions in the eastern tropical Pacific. (b) Ordination showing 95% confidence limits of selected species. These two axes represent 94% of the species-environment variance, 15% of the total encounter rate variance.

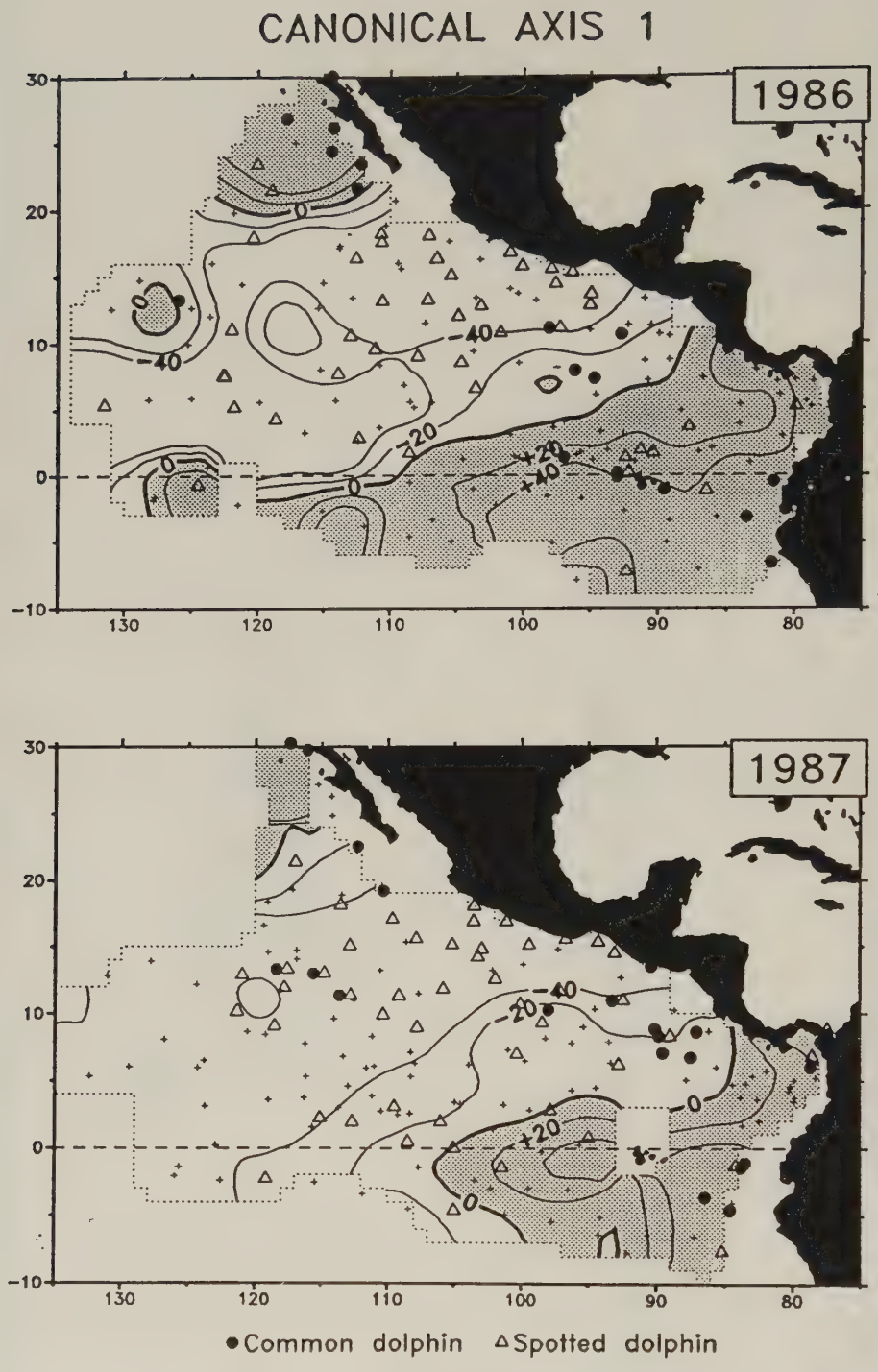


Figure 6. Maps of distribution of canonical axis 1 for 1986-1989. Positive areas are shaded. Spotted dolphin sighting localities are shown as open triangles, common dolphin localities as closed circles. A "+" represents a sighting day during which neither spotted nor common dolphins were seen.

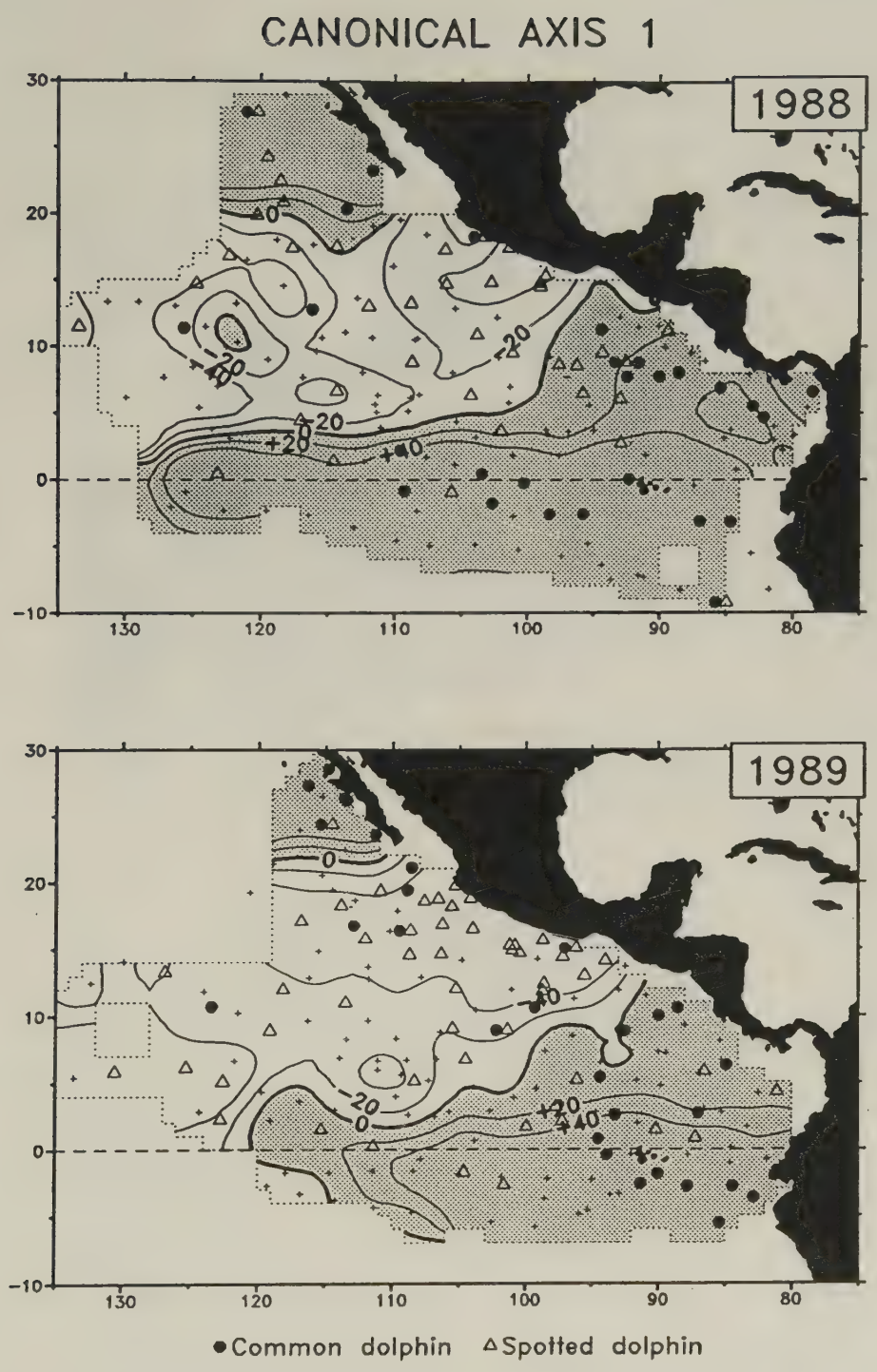


Figure 6. (Continued) - Maps of distribution of canonical axis 1 for 1986-1989. Positive areas are shaded. Spotted dolphin sighting localities are shown as open triangles, common dolphin localities as closed circles. A "+" represents a sighting day during which neither spotted nor common dolphins were seen.

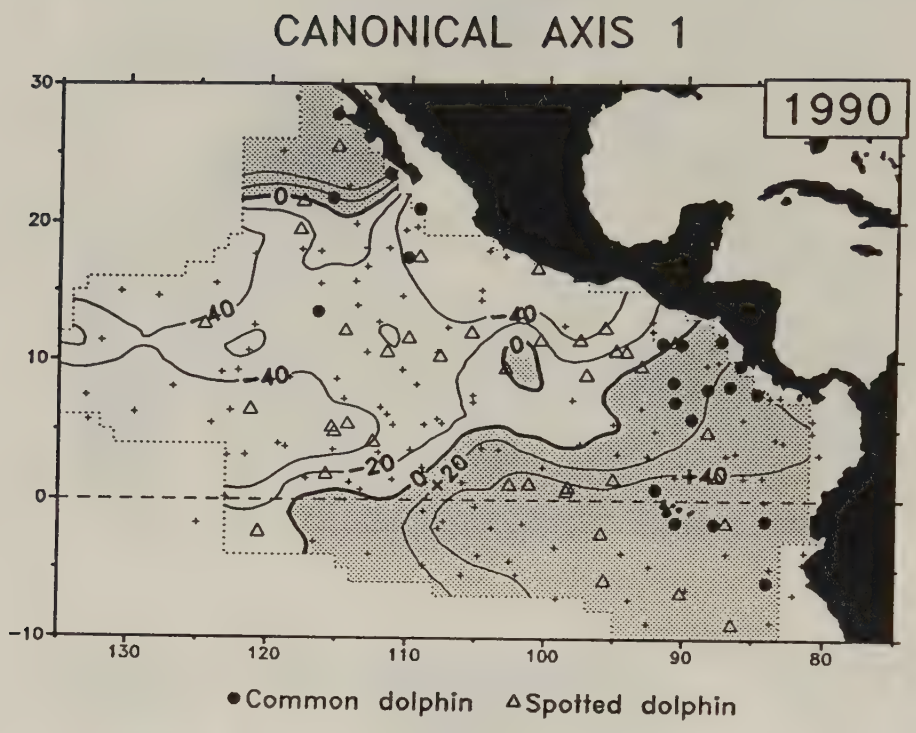


Figure 6. (Continued) - Maps of distribution of canonical axis 1 for 1986-1989. Positive areas are shaded. Spotted dolphin sighting localities are shown as open triangles, common dolphin localities as closed circles. A "+" represents a sighting day during which neither spotted nor common dolphins were seen.

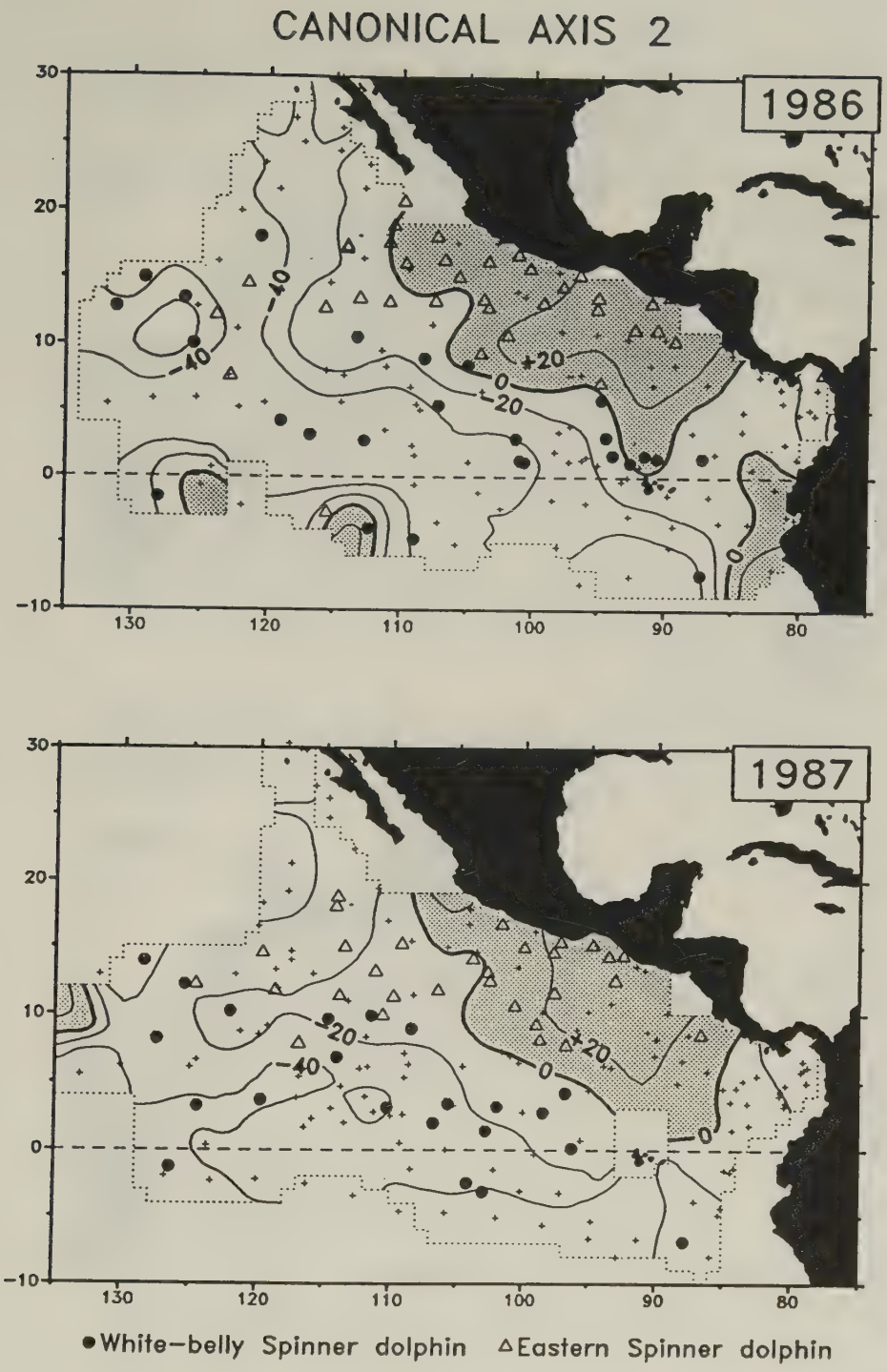


Figure 7. Maps of distribution of canonical axis 2 for 1986-1990. Negative areas are shaded. Eastern spinner sighting localities are represented by closed circles, whitebelly spinner localities by open triangles.

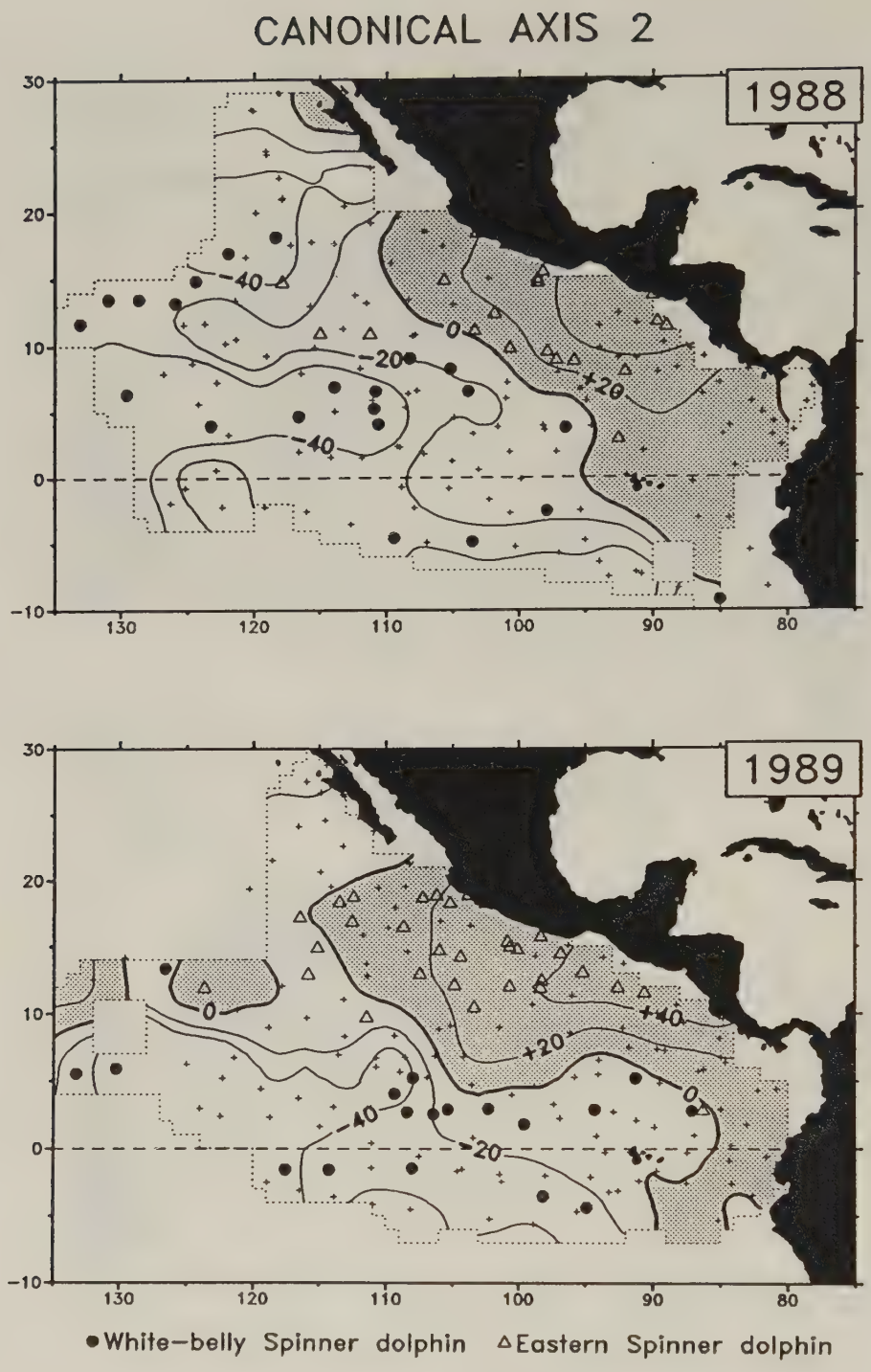


Figure 7. (Continued) - Maps of distribution of canonical axis 2 for 1986-1990. Negative areas are shaded. Eastern spinner sighting localities are represented by closed circles, whitebelly spinner localities by open triangles.

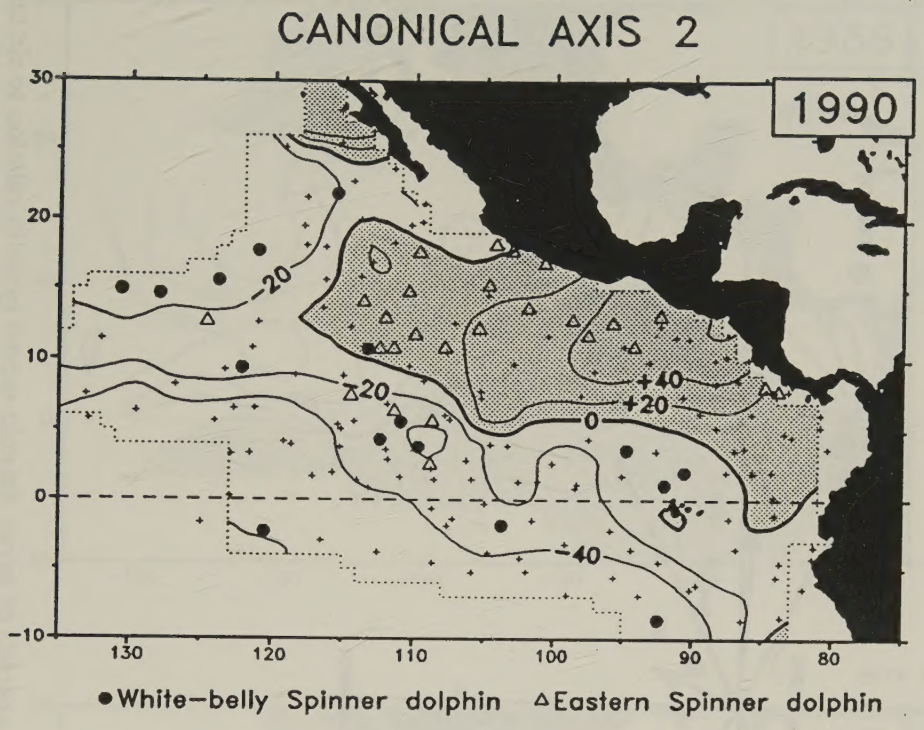


Figure 7. (Continued) - Maps of distribution of canonical axis 2 for 1986-1990. Negative areas are shaded. Eastern spinner sighting localities are represented by closed circles, whitebelly spinner localities by open triangles.

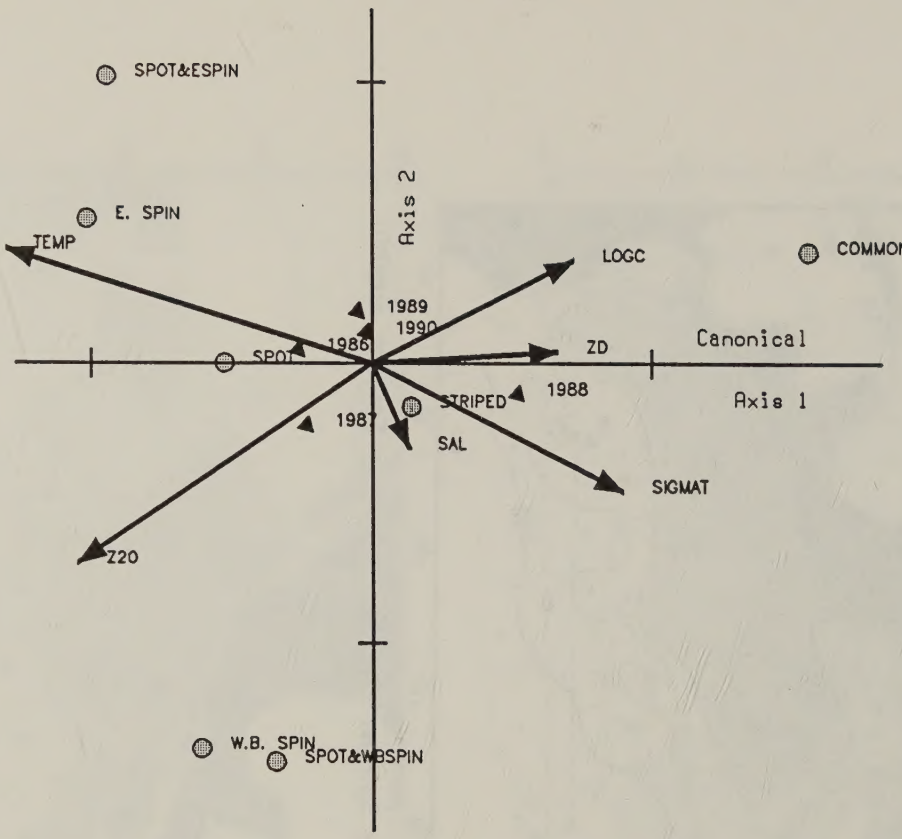


Figure 8. Ordination biplot from canonical correspondence analysis of seven dolphin school types in relation to six oceanographic variables (see Fig 5 for definitions), with five sample years as categories. Mean values for each year are represented by triangles, YEAR 1 = 1986, YEAR 2 = 1987, etc.

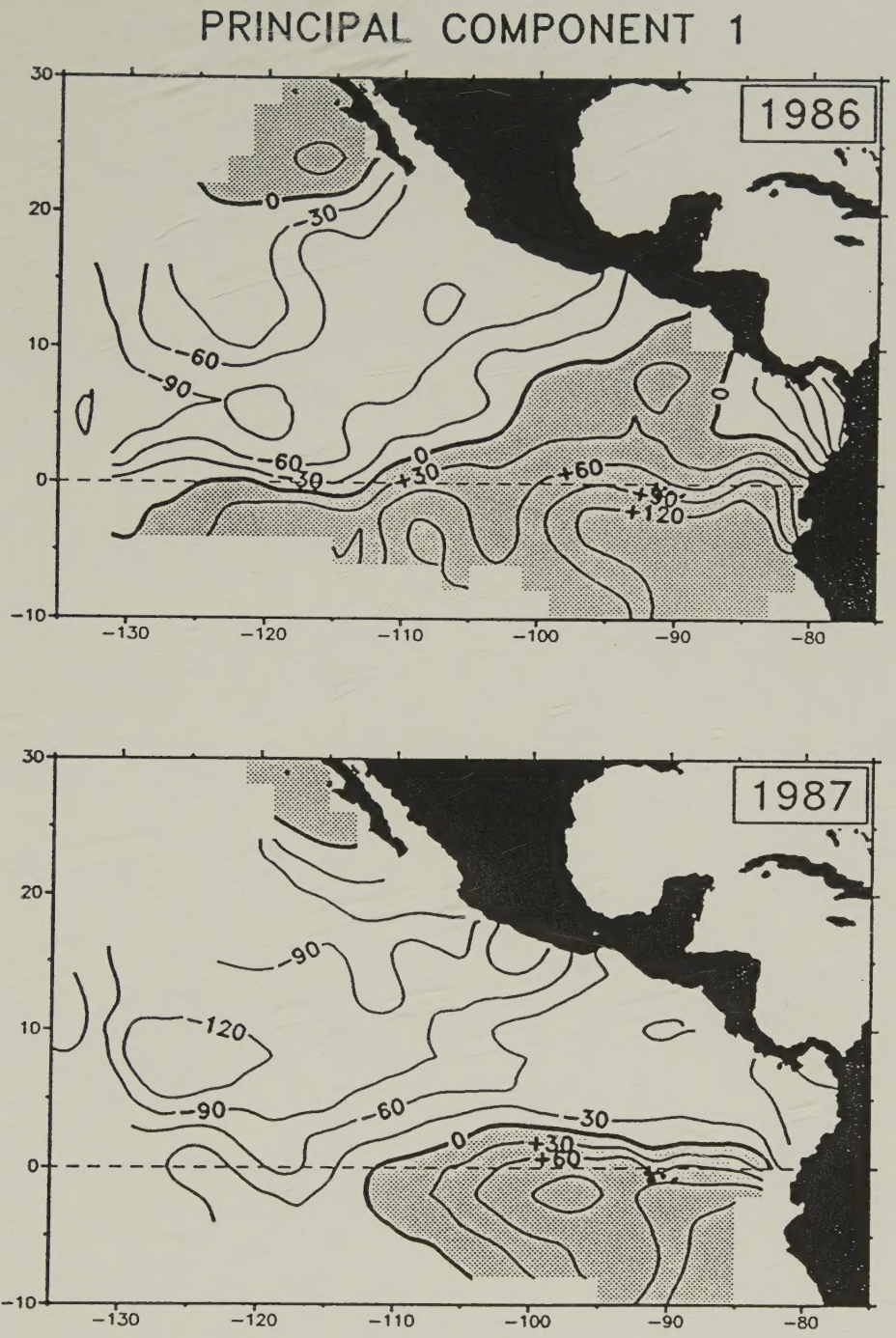


Figure 9. Maps of distribution of principal component 1 from environmental data collected during 1986-1987, for comparison to CCA axis 1 shown in Fig. 6.